

## A Photoperiod Determined Life-Cycle in an Oligochaete Worm

BERND SCHIERWATER<sup>1</sup> AND CARL HAUENSCHILD

*Zoologisches Institut der Technischen Universitaet, Pockelsstr. 10a,  
3300 Braunschweig, West Germany*

**Abstract.** For one common cosmopolitan naidid worm, *Stylaria lacustris*, we studied the effects of different environmental factors upon (1) the alternation of reproductive modes, (2) the rates of population increase, and (3) the combination of each of (1) and (2). While age, temperature, population density, or rate of feeding did not affect the mode of reproduction, photoperiod had a dominant effect. Under long-day conditions (LD > 12:12), all worms reproduced exclusively by paratomic fission, theoretically *ad infinitum*. When transferred to short-day conditions (LD ≤ 12:12) the worms ceased vegetative reproduction, and within 2 to 4 weeks developed the hermaphroditic genital apparatus and a clitellum. After an additional two weeks, the first cocoons were produced. The switch to the bisexual mode of reproduction was *cum grano salis* irreversible. These findings are consistent with observations of field samplings, and allow one to predict the annual life-cycle strategy of *S. lacustris*. This is the first example of a photoperiod determined life-cycle within the oligochaete worms.

The vegetative mode of reproduction led to extremely high rates of population increase, whereas with the bisexual mode of reproduction the number of individuals was roughly stable. However, because *S. lacustris* could not withstand temperatures of 5°C or lower, the switch to sexual reproduction and the formation of diapausing cocoons appear to be the only mechanism of overwintering. Nevertheless, some 'asexual' clones never switch to sexual reproduction, whereas a loss of the asexual vegetative mode of reproduction did not occur. In contrast to some general predictions from life-history theories, the reproductive strategy of *S. lacustris* is highly repro-

grammed and cannot respond to sudden and unexpected environmental changes.

### Introduction

With the pollution of our environment, present day ecology demands investigation of the biological mechanisms that regulate the distribution and dynamics of populations in a given environment (*e.g.*, Brinkhurst and Jamieson, 1971; McElhone, 1978; Brinkhurst and Cook, 1980; Tauber *et al.*, 1986; Zaslowski, 1988; Klerks and Levington, 1989). The rapid increase in theories on the evolution of life histories demands extended experimental work and empirical data (*cf.* Stearns, 1976, 1980; Reznick, 1985; Hoekstra, 1987; Michod and Levin, 1988; Hauenschild, 1989; Nunney, 1989).

The study of particular oligochaete worms can be highly fruitful to our understanding of both the ecological and the evolutionary implications of animal life-cycles for two reasons: (1) the oligochaete worms in general are regarded as perhaps the most important group concerned with the retrieval of organic matter in freshwaters (*e.g.*, Brinkhurst and Jamieson, 1971; Dumnicka and Pasternak, 1978; Brinkhurst and Cook, 1980). (2) Those oligochaete worms that are capable of reproducing both by a bisexual and by a vegetative mode of reproduction, in particular the Aeolosomatidae and Naididae, allow *intraspecific* comparisons of the consequences of sexual *vs.* asexual life-history tactics; such systems allowing experimental work are badly needed but are difficult to find (*cf.* Bell, 1980; Townsend and Calow, 1981; Calow, 1983; Reznick, 1985; Hoekstra, 1987; Abugov, 1988; Schierwater, 1989; Hadrys *et al.*, 1990). Unfortunately, the number of well understood life-cycles that include an 'alternation of reproductive modes,' is surprisingly low (*cf.*, Giese, 1959; Giese and Pearse, 1959; Kinne, 1970; Brinkhurst and Cook, 1980; Townsend and Calow, 1981; Holm, 1988).

Received 13 November 1989; accepted 2 January 1990.

<sup>1</sup> Present address: Yale University, Department of Biology, P.O. Box 6666, New Haven, CT 06511.

Records of the reproductive ecology of most oligochaetes are limited to notes on the presence of sexually mature specimens in field populations, but almost no conclusions can be drawn from these scattered notes; thus, little is known about the mechanisms affecting the mode of reproduction and hence their annual life-cycles (e.g., Vershinin and Semernoi, 1977; McElhone, 1978, 1982; Mill, 1978; Brinkhurst and Cook, 1980; Pascar-Gluzman, 1981; Wetzel, 1982).

In this study we will present the annual life-cycle model as well as quantitative data on the consequences of sexual vs. asexual reproduction for the cosmopolitan naidid *Stylaria lacustris* Linnaeus 1758. Its life-cycle has not been described, though growth rates of vegetative worms have been studied (Streit, 1978; McElhone, 1982; Finogenova, 1984) and several brief notes about sexual worms are available (Kamlyuck and Kovaltchuk, 1972; McElhone, 1978, 1982; Wetzel, 1982). McElhone (1982) suggested that food supply, food quality, and water quality may affect the 'alternation of reproductive modes' in *S. lacustris*. In this study we will demonstrate that the life cycle of *S. lacustris* is strictly and exclusively determined by the photoperiod (day-length). We shall discuss this first finding of a photoperiod-determined life-cycle in an oligochaete worm in an ecological context regarding the evolution of the life-history strategy.

## Materials and Methods

### Animals

*Stylaria lacustris* is one of the most common and widely distributed oligochaete species, found in Europe, Asia, Africa, and North America (e.g., Brinkhurst and Jamieson, 1971; Vershinin and Semernoi, 1977; McElhone, 1978; Pascar-Gluzman, 1981; Wetzel, 1982). In *S. lacustris*, the vegetative mode of reproduction follows the type of paratomic fission of animal chains of between two to three individuals (Stephenson, 1930). The biology of sexual reproduction has not been described.

Worms were counted as 'sexual' if either gonads and/or a clitellum were visible. All other worms were called 'vegetative' independent of the formation of tomites.

### Field samples

All animal material of *Stylaria lacustris* was collected from the field at different times and transferred into the laboratory for culturing under defined laboratory conditions. Worms were collected in W. Germany from a pond at Weddel, Braunschweig, in July 1985, Sept. and Oct. 1987, June and July 1988, and from the river Ilmenau at Uelzen in August 1986, '87, '88. Right after sampling, as many worms as possible were isolated and checked within 24 h for their reproductive status (i.e.,

presence or absence of a clitellum, gonads, tomites) by means of a dissection microscope at 20 $\times$ .

### Laboratory studies

Under defined laboratory conditions, we investigated whether the following environmental factors influence the 'alternation of reproductive modes': temperature, feeding, population density, and photoperiod.

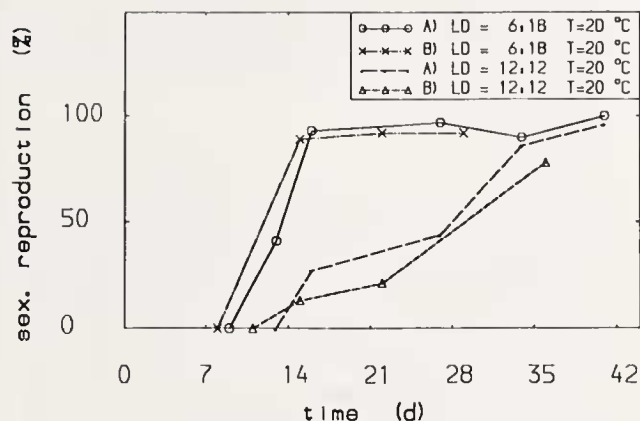
**Culturing.** Culture dishes (400 cm<sup>3</sup> 'deep freeze' plastic containers) were kept in thermoregulated rooms or in chambers providing temperature constancy to  $\pm 1^\circ\text{C}$ , as controlled by mini-max-thermometers; normal photoperiod setting was LD = 16:8, unless otherwise stated. *S. lacustris* was cultured either in filtered and heated (2 h at 80 $^\circ\text{C}$ ) water of its natural environment, or in carbonic-acid-free natural mineral water ('Vittel' or 'Volvic'). Worms were fed on the green algae *Haematococcus lacustris* and *Gonium sociale ad lib*. The air bubbled culture dishes were washed, and water and food were renewed twice a week.

Acclimation time to any new experimental condition was 24 h. The highest changes in temperature were 5 $^\circ\text{C}$  per day. Temperature changes of 10 $^\circ\text{C}$  were done stepwise within 4 days. For long-period observations on the reproductive activity under different feeding, temperature, and photoperiod conditions, acclimation time was 14 days, unless otherwise stated.

Animals were observed through a binocular microscope ('Zeiss' 475052-9901) with variable magnifications from 8 $\times$  to 50 $\times$ . One ocular was equipped with a  $\mu\text{m}$ -scale for *in vivo* measurements of one-dimensional distances.

**Photoperiod settings.** Experiments on the effects of photoperiod on the mode of reproduction were run at 20  $\pm 1^\circ\text{C}$ , unless otherwise stated. The following LD settings were used: LD = 6:18, 12:12, 16:8, 18:6, and 24:0. Light intensities were 500–2000 lx during light periods and  $\approx 0.05$  lx in the dark, respectively. The light intensities were measured with a lightmeter (Gossen, Mavolux 6C 18493), and because of the use of fluorescent lights (Osram L40W/22-1), the light intensity values have to be taken with care. During all experiments and observations on the effects of temperature, feeding rate, population density and age, light-dark rhythm was held constant at LD = 16:8.

**Mean doubling times.** For observations on mean doubling times (mdt), 30 worms each were placed in plastic chambers of  $\approx 400$  cm<sup>3</sup>, and the number of worms per chamber was counted once a week. After each counting, the total number of worms was reduced to a maximum of 50 worms per chamber. Two populations (one from Weddel pond and one from the river Ilmenau) were followed over 8 weeks (2 weeks acclimation plus 6 weeks of registration) at 10, 15, 20, and 25 $^\circ\text{C}$ . The mdt's were



**Figure 1.** Examples for the time course of switching from the vegetative to the bisexual mode of reproduction induced by the photoperiod in *Stylaria lacustris*. Vegetatively reproducing worms from the field were exposed to short-day conditions of either LD = 12:12 or LD = 6:18 at day 0 in the figure; A = Weddel 1985, B = Ilmenau 1986 population; the points for LD = 16:8 are not shown, for all of them would lie along the abscissa (= 0% sexual reproduction); N > 1000 for each population.

calculated from the initial population size ( $N_1$ ), the final population size ( $N_2$ ) and the time ( $t$ ) in days between the countings:  $mdt = \log 2 / (\log N_2 - \log N_1)$ .

**Statistics.** The non-parametric Mann-Whitney-U test (two-tailed) was used to compare the means of two independent samples, and the Jonckheere test was used to look for monotonous trends in three or more independent samples (Lienert, 1976). The number of statistical replicates (*i.e.*, number of cultures tested under the same experimental conditions) is given as  $n$  in the text, whereas  $N$  means the total number of worms checked for their reproductive mode during one experiment.

## Results

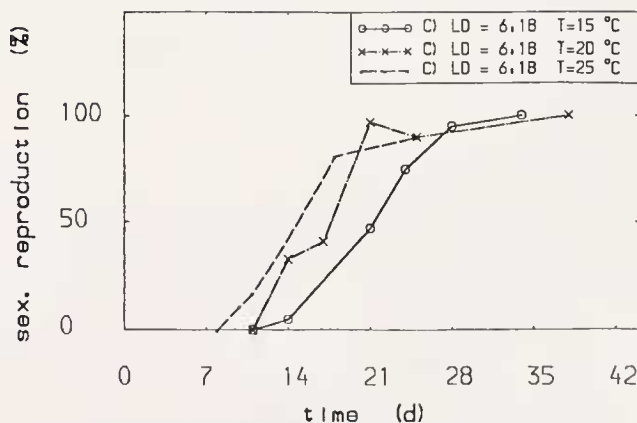
### Photoperiod

The mode of reproduction was strictly determined by the photoperiod. Under long-day conditions (LD > 12:12) the worms reproduced exclusively vegetatively by paratomic fission. Exposure to short-day conditions (LD ≤ 12) induced a quantitative switch from paratomic fission to sexual reproduction within 10 to 30 days (Fig. 1), *i.e.*, the hermaphroditic genital apparatus has been developed. The formation of the clitellum always occurred after the gonads became visible (in some cases up to 25 days later). The reaction time to the short-day condition, *i.e.*, for the switch in the mode of reproduction, was affected by the temperature. One population was divided into three portions and each portion cultured at either 15, 20, or 25°C. With increasing temperature the time for switching from the vegetative to the sexual mode of reproduction was significantly shortened ( $P \leq 0.001$ , Jonckheere,  $N = 3 \times 38$ ; see Fig. 2).

The alternation of reproductive mode worked only in one direction, *i.e.*, only vegetative worms switched to sexual reproduction. Once this switch had occurred, it was *cum grano salis* irreversible. Ninety-one clitellate worms had been transferred back from LD = 6:18 to LD = 16:8 ( $T = 20^\circ\text{C}$ ) and watched for 42 continuous days. Only three worms reverted to vegetative asexual reproduction by forming tomites; in these three worms the clitellum of the parent individual was retained, whereas the daughter individuals showed normal asexual shape.

Bisexual reproduction excluded fission, *i.e.*, clitellate worms never formed tomites. Therefore, once a population became sexual, the number of worms per chamber became constant or even declined slightly, because some worms always died after changing the photoperiod. Under laboratory conditions, the number of cocoons produced per sexual worm was low at all tested temperatures. Rates of cocoon production ranged from 0.25 to 2.0 cocoons per sexual worm until death. The highest rates of cocoons produced per sexual worm, within 3 weeks after the clitellum became visible, were 0.5 ( $T = 15^\circ\text{C}$ ), 0.7 ( $T = 20^\circ\text{C}$ ), and 0.8 ( $T = 25^\circ\text{C}$ ). Generally the first cocoons were produced at  $16.3 \pm 5.61$  days (range 7–31 days;  $N = 650$ ,  $n = 13$ ) after clitellum formation. Bisexual reproduction thus led to a very limited rate of production of reproductive units. Cocoons were lemon-shaped and preferably placed in the corners of the culture dishes. Mean  $\pm$  SD cocoon length was  $0.8 \pm 0.07$  mm ( $n = 78$ ), and each cocoon contained a maximum of three embryos.

**Asexual clones.** Two culture populations of *S. lacustris* that came from the Weddel pond and had been cultured exclusively vegetatively ( $T = 20^\circ$ , LD = 16:8) over 14 or 23 months, respectively, failed to show a photoperiodic



**Figure 2.** Example of the effect of temperature on the time course of switching from the vegetative to the bisexual mode of reproduction in *Stylaria lacustris*; one vegetative population (C = Weddel 1988) of 114 worms was divided into 3 portions, and each group of 38 worms was exposed to one of three different temperatures under short-day conditions (LD = 6:18) at day 0.

Table I

The mean doubling times (mdt) of vegetatively reproducing *Stylaria lacustris* at different experimental temperatures

T [°C]	N	n	mdt [d]	range	
				min	max
10	277	7	11.1 ± 4.04	9.3	16.9
15	657	12	6.9 ± 2.47	4.8	10.9
20	733	12	5.1 ± 2.83	2.7	13.2
25	854	12	5.0 ± 3.49	2.5	14.4

The means ± SD and the ranges over a 6-week observation period of each two cultures are given. At 10°C, one culture died after the first week of observation period, hence here n = 7.

reaction. Samples of each population were tested at both LD = 12:12 and LD = 6:18 each at 15°C and 20°C over 13 weeks. From 238 worms, only 8 worms, i.e., ≈3%, became sexually mature.

*Mean doubling times for vegetative populations.* The differences in mdt between the Weddel and the Ilmenau populations were not significant (U-test) and hence the groups were pooled in Table I. The mdt decreased significantly with increasing temperature ( $P \leq 0.05$ , Jonckheere). However, the differences between 20°C and 25°C were not significant (U-test).

#### Other environmental factors

No *S. lacustris* worm reproduced sexually when the light period was  $\geq 12$  h per day. Thus, the mode of reproduction was independent of temperature, feeding and population density, and age (see Table II).

*Temperature.* Different populations of *S. lacustris* were exposed to temperatures between 5 and 30°C for 14 weeks. Temperatures of 5°C and 30°C were not tolerated, and all experimental animals died within 6 days ( $N = 2 \times 63$ ,  $n = 2 \times 3$ ). In the zone of thermal-tolerance, not one sexually reproducing individual was found ( $N > 1000$ ) during 14 weeks of observation. One culture at 10°C was cultured for another 9 weeks and checked 3 times per week. On 10 October 1988 (after 21 weeks in controlled conditions), two worms were found that had a well developed genital apparatus and a clitellum. Neither worm was found after two weeks; their fate is unknown. Cocoons were not found.

*Feeding.* Feeding rates reduced to 3 days feeding per week over 10 weeks never led to a sexual worm. All worms kept reproducing vegetatively ( $N > 600$ ,  $n = 3$ ). Starvation experiments, resulting in LD<sub>50</sub> values of  $18 \pm 3.75$  days (range for total population extinction: 20–31 days), also never led to sexually reproducing worms ( $N = 100$ ,  $n = 3$ ; T = 20°C, LD = 16:8).

*Population density.* Different population densities of

0.1–1.5 worms cm<sup>-2</sup> bottom area of culture dish were tested over 10 weeks at T = 20°C. No sexual worms were found ( $N > 1000$ ,  $n = 3$ ).

#### Field samples

Field samples of *S. lacustris* were taken at different times of the year. Only in one sample, collected in October 1987, were both vegetative as well as sexual worms found. In all other samples collected between June and September exclusively acitellate worms were found (see Table III). The only exception was observed on 19 August 1988. Two clitellate worms were detected in a field sample from the Weddel pond collected on 17 July 1988. The sample (including plant material) had been stored in a plastic beaker in our laboratory for four weeks at natural daylight. Other worms found in the sample were acitellate ( $N = 108$ ) on 19–21 August.

#### Discussion

Although studies of the seasonal development of organisms have always occupied an important place in experimental biology, the leading role of the signaling factors in determining seasonal phenomena have been largely unknown. For *S. lacustris*, the results of this study unmistakably demonstrate that the life-cycle is strictly determined by the photoperiod as the relevant external signaling factor. Since the outstanding discoveries of Garner and Allard (1920) and Rowan (1926) on photoperiodic phenomena in plants and animals, many important contributions have derived from studies in particular on polychaetes and insects (for overview see Giese, 1959; Kinne, 1970; Segal, 1970; Hauenschild, 1975; Tauber *et al.*, 1986; Zaslowski, 1988), but none from the phylogenetically closely related oligochaetes.

#### The alternation of reproductive modes

*Stylaria lacustris* apparently measures the day-length (proximate factor) to prepare for the sharp temperature decline (ultimate factor) during winter. Under long-day (summer) conditions, the worms reproduced exclusively asexually by paratomic fission, theoretically *ad infinitum*. In the 1960's, Hauenschild (unpubl.) cultured a population of *S. lacustris* for more than six continuous years in the laboratory at LD = 16:8 and T = 20°C, and he did not find a single sexually mature worm during this period. In the short-day (autumn conditions), *S. lacustris* reproduces only once and then the worms die. Hence, *S. lacustris* can best be termed as a 'continuous asexual and monotelic bisexual breeder' (using the terminology as reviewed by Mill, 1978).

The two findings of sexual worms of unknown origin under long-day conditions can hardly weaken the results. However, the two observed asexual populations that al-

Table II

The effects of age and different environmental factors on the switch from vegetative to bisexual reproduction in *Stylaria lacustris*

	Age	Temperature	Pop. dens.	Feeding rate	Short-day
$N_{veg}$ (n)	>1000 (5)	>1000 (5)	>1000 (3)	>600 (3)	>1000 (5)
time [d]	98	98	70	70	21-36
sexual [%]	0	0	0	0	>95

$N_{veg}$  = initial number of vegetative worms exposed to the conditions listed.

(n) = Number of different populations tested.

time = Observation time.

Short-day = LD  $\leq$  12:12. The photoperiod (short-day) is the only factor found to determine the switch from the vegetative to the bisexual mode of reproduction. Under long-day conditions the worms never became sexually mature (as followed continuously over more than 20 generations), independent of temperature, population density (pop. dens.) and feeding rate.

most did not switch to sexual reproduction under short-day conditions are noteworthy. It is unknown whether an irreversible genetically based loss of sexuality or some kind of 'permanent modification' had occurred in these populations. The latter was first observed by Hauenschild (1956, 1957) in the anthomedusae of *Eleutheria dichotoma* from the Mediterranean. Here, a small percentage of primary medusae directly budded off from the polyp was regularly found to be asexual. In the field a loss of the sexual mode of reproduction is known from the sedentary polychaete *Ctenodrilus serratus*. In the North Sea, *C. serratus* reproduces exclusively asexually by paratomic fission, whereas in the Mediterranean Sea sexually mature (hermaphroditic) worms are known. In *S. lacustris*, asexual clones were only found in populations that had been cultured vegetatively for a long time in the laboratory (here, more than 14 or 23 months, respectively). Whether field samples also include a small percentage of asexual clones cannot be answered, because some worms always died when changing the photoperiod from long- to short-day. In the field, the asexual clones would go extinct whenever the temperature dropped below 5°C, i.e., normally during the winter in

the Palaearctic area. Only the 'normal' clones showing the photoperiodic reaction can survive. However, in biotopes showing annual temperature fluctuations between only 10°C and 25°C, a loss of the bisexual mode of reproduction in field populations of *S. lacustris* seems likely, analogous to the polychaete *C. serratus*. If those habitats are found this can be easily tested by exposing population samples to short-day conditions.

#### The annual life-cycle

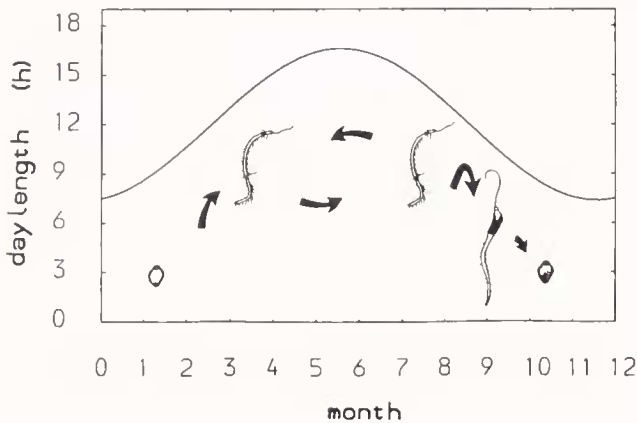
From the findings of this study, the life-cycle of *S. lacustris* can be roughly described as shown in Figure 3. The prediction is rough in the sense that the tested LD scalings were broad and the within-population genetic variation is unknown. The predicted life-cycle from this study allows *S. lacustris* to start sexual reproduction and hence production of diapausing cocoons prior to, and in anticipation of, the cold winter period, which is critical for the worms' survival (cf. Denlinger *et al.*, 1978; Ingrisch, 1984; Zaslowski, 1988). At 52°N. lat. this would be from October to November, corresponding to the natural habitats in north Germany, where ponds usually do

Table III

Proportions of reproductive modes in field samples of *Stylaria lacustris*

Date	Place	N	Sex [N]	Veg [N]	{ } [N]	Clit [%]	Aclit [%]
14 July 1985	pond Weddel	26	0	11	15	0	100
10 Aug. 1986	river Ilmenau	161	0	68	93	0	100
30 Aug. 1987	river Ilmenau	107	0	57	50	0	100
20 Sept. 1987	pond Weddel	4	0	1	3	0	100
16 Oct. 1987	pond Weddel	48	41	0	7	85	15
12 June 1988	pond Weddel	96	0	53	43	0	100

Samples were taken from different plants (e.g., of the genera *Ceratophyllum*, *Chara*, *Elodea*, *Nasturbium*) from a pond at Weddel (near Braunschweig) or from the river Ilmenau near Uelzen (Niedersachsen, W. Germany); Oct. 16, 1987 is the only sample collected under natural short-day conditions; { } refers to individuals in which no kind of actual reproduction was obvious; Clit and Aclit refer to clitellate and aclitellate individuals, respectively.



**Figure 3.** The annual life-cycle of *Stylaria lacustris*. The external signaling factor daylength is given for 52°N. lat. The laboratory studies and field samples suggest that the switch from asexual paratomic fission to bisexual reproduction occurs in mid September at this latitude. About three weeks later the first worms become sexually mature, and the first diapausing cocoons are produced during October. Further explanations are given in the text.

not freeze before December. The genetic variation within and between populations would be the predicted basis for adapting *S. lacustris* to different annual cycles with respect to temperature and photoperiod (e.g., Sauer, 1977; Sauer *et al.*, 1986; Groeters and Dingle, 1987). This could be tested by collecting *S. lacustris* at different latitudes with similar annual temperature cycles, or at different altitudes with similar annual photoperiod cycles, and measuring the threshold for the photoperiodic reaction (cf. Hairston and Olds, 1984, 1986).

#### 'All or nothing' life-history strategy

By using the vegetative mode of reproduction, *S. lacustris* can double its number at least every 5 days at 20 to 25°C (Table 1). Data on the rates of population increase by vegetatively reproducing populations of *S. lacustris* given in the literature range from mean doubling times of 3.6 to 12 days between 15°C and 20°C (Streit, 1978; McElhone, 1982; Finogenova, 1984). The data agree with Streit (1978), who calculated mdt of 3.6 ( $T = 19^\circ\text{C}$ ) and McElhone (1982), who estimated values of 4–6 days ( $T = 20^\circ\text{C}$ ). In the latter case it is not clear whether these are mean values or maximal values. During summer all efforts are invested in vegetative reproduction, leading to the most rapid population increases, regardless of the actual physical environmental conditions (r-strategy); during one season (April through September) one single worm can theoretically give rise to a population of 3.4 billion worms. During autumn all effort is invested in sexual reproduction, *i.e.*, the number of cocoons produced for overwintering is maximized, regardless of whether the winter temperatures go below 5°C

or not. An unexpected and abnormal temperature decline to  $\leq 5^\circ\text{C}$  during summer or early autumn would lead to the total extinction of populations. Furthermore, the reproductive strategy cannot respond to unexpected changes in other environmental factors, like food supply and population density. Therefore, the life-cycle strategy of *S. lacustris* is an 'all or nothing' strategy maximizing reproductive output as far as possible (cf. Hirshfield and Tinkle, 1975; Pianka, 1976; Stearns, 1976). This is consistent with a high degree of adaptation to predictable annual cycles of environmental conditions; thus the life history strategy of *S. lacustris* does not fulfill some predictions from life history theories. In a fluctuating and unpredictable environment (such as small freshwater ponds), we would expect *S. lacustris* (a) to reach early sexual maturity, instead of postponing it as far as possible to the end of the season or (b) to show reproductive flexibility in order to minimize the risk of total failure in a bad year (cf. Stearns, 1976, 1980; Glesener and Tilman, 1978; Mill, 1978; Sauer, 1984; Groeters and Dingle, 1987).

The high abundances and the wide distribution of *S. lacustris*, however, indicate that the photoperiodic life-cycle strategy can also be very successful in oligochaetes. It seems unlikely that *S. lacustris* should be the only oligochaete worm that has been found to synchronize its life-cycle with the seasons of the year by measuring daylength, and it might be reasonable to look for photoperiodic reactions in other oligochaete worms that perform an alternation of reproductive modes.

#### Acknowledgments

We thank Hansi Fauter, Heike Fee Hadrys, and Dr. D. Teschner (all Braunschweig). We are indebted to Prof. L. W. Buss, Dr. N. W. Blackstone, and Matt Dick (all Yale) for their critical comments and corrections on earlier versions of the manuscript. The work was supported by a grant from 'GradFoeg des Landes Niedersachsen,' W. Germany.

#### Literature Cited

- Abugov, R. 1988. A sex-specific quantitative genetic theory for life-history and development. *J. Theor. Biol.* 132: 437–442.
- Bell, G. 1980. The costs of reproduction and their consequences. *Am. Nat.* 116: 45–76.
- Brinkhurst, R. O., and B. G. M. Jamieson. 1971. *Aquatic Oligochaeta of the World*. Oliver & Boyd, Edinburgh. 860 pp.
- Brinkhurst, R. O., and D. G. Cook, eds. 1980. *Aquatic Oligochaete Biology*. Plenum Press, New York. 530 pp.
- Calow, P. 1983. Energetics of reproduction and its evolutionary implications. *Biol. J. Linn. Soc.* 20: 153–165.
- Denlinger, D. L., C. P. Chen, and S. Tanaka. 1978. The impact of diapause on the evolution of other life-history traits in flesh flies. *Oecologia* 77: 350–356.
- Dumnicka E., and K. Pasternak. 1978. The influence of physico-chemical properties of water and bottom sediments in the river

- Nida (Poland) on the distribution and number of oligochaeta. *Acta Hydrobiol.* **20**: 215–232.
- Finogenova, N. P. 1984.** Growth of *Stylaria lacustris* (L.) (Oligochaeta, Naididae). *Hydrobiol.* **115**: 105–107.
- Garner, N. H., and A. H. Allard. 1920.** Effect of the relative length of day and night and other factors of the environment on growth and reproduction in plants. *J. Agricult. Res.* **18**: 553–606.
- Giese, A. C. 1959.** Comparative physiology: annual reproductive cycles of marine invertebrates. *Ann. Rev. Physiol.* **21**: 547–576.
- Giese, A. C., and J. S. Pearse, eds. 1959.** *Reproduction of Marine Invertebrates*. Vol. I. Academic Press, New York.
- Glesener, R. R., and D. Tilman. 1978.** Sexuality and the components of environmental uncertainty: clues from geographic parthenogenesis in terrestrial animals. *Am. Nat.* **112**: 659–673.
- Groeters, F. R., and H. Dingle. 1987.** Genetic and maternal influences on life history plasticity in response to photoperiod by milkweed bugs (*Oncopeltus fasciatus*). *Am. Nat.* **129**: 332–346.
- Hadrys, H., B. Schierwater, and W. Mrowka. 1990.** The feeding behaviour of a semi-sessile hydromedusa and how it is affected by the mode of reproduction. *Anim. Behav.* (in press)
- Hairston, N. G., Jr., and E. J. Olds. 1984.** Population differences in the timing of diapause: adaptation in a spatially heterogeneous environment. *Oecologia* **61**: 42–48.
- Hairston, N. G., Jr., and E. J. Olds. 1986.** Partial photoperiodic control of diapause in three populations of the freshwater copepod *Diaptomus sanguineus*. *Biol. Bull.* **171**: 135–142.
- Hauenschild, C. 1956.** Experimentelle Untersuchungen ueber die Entstehung asexueller Klone bei der Hydromeduse *Eleutheria dichotoma*. *Z. Naturf.* **11b**: 394–402.
- Hauenschild, C. 1957.** Ergaenzende Mitteilung ueber die asexuellen Medusenklone bei *Eleutheria dichotoma*. *Z. Naturf.* **12b**: 412–413.
- Hauenschild, C. 1975.** Die Beteiligung endokriner Mechanismen an der geschlechtlichen Entwicklung und Fortpflanzung von Polychaeten. *Verh. Deutsch. Zool. Ges.* **67**: 292–308.
- Hauenschild, C. 1989.** Book review: Stearns, S. C., ed. 1987. *The Evolution of Sex and its Consequences*. Birkhaeuser, Basel. *Ethology* **88**: 335–336.
- Hirshfield, M. F., and D. Tinkle. 1975.** Natural selection and the evolution of reproductive effort. *Proc. Nat. Acad. Sci. USA* **72**: 2227–2231.
- Hoekstra, R. F. 1987.** The evolution of sexes. Pp 59–91 in *The Evolution of Sex and its Consequences*. Stearns S. C., ed. Birkhaeuser, Basel.
- Holm, E. 1988.** Environmental restraints and life strategies: a habitat templex matrix. *Oecologia* **75**: 141–145.
- Ingrisch, S. 1984.** The influence of environmental factors on dormancy and duration of egg development in *Metrioptera roeseli* (Orthoptera: Tettigoniidae). *Oecologia* **61**: 254–258.
- Kamlyuck, L. V., and M. M. Kovalchuk. 1972.** Some data about number, growth and production of oligochaete *Stylaria lacustris* (Naididae, Oligochaeta) in littoral lake Narotch. Pp. 148–151 in *Aquatic Oligochaeta* All Union Symposium, Borok 27–30 June 1972, Jaroslavl. (Russ.).
- Kinne, O., ed. 1970.** *Marine Ecology*. Vol I, part I. Wiley, New York. 681 pp.
- Klerks, P. L., and J. S. Levinton. 1989.** Rapid evolution of metal resistance in a benthic oligochaete inhabiting a metal-polluted site. *Biol. Bull.* **176**: 135–141.
- Krehan, J. 1970.** Die Steuerung von Jahresrhythmik und Diapause bei Larval- und Imagnalueberwinterern der Gattung *Pterostichus* (Col., Carab.) *Oecologia* **6**: 58–105.
- Lienert, G. A. 1976.** *Verteilungsfreie Methoden in der Biostatistik*. Bd. I. Anton Hain, Meisenheim a.Gl.
- McElhone, M. J. 1978.** A population study of littoral dwelling Naididae (Oligochaeta) in shallow mesotrophic lakes in North Wales. *J. Anim. Ecol.* **47**: 615–626.
- McElhone, M. J. 1982.** The distribution of Naididae (Oligochaeta) in the littoral zone of selected lakes in North Wales and Shropshire. *Freshwater Biol.* **12**: 421–425.
- Michod R. E., and B. R. Levin, eds. 1988.** *The Evolution of Sex. An Examination of Current Ideas*. Blackwell Scientific, Oxford. 342 pp.
- Mill, P. J., ed. 1978.** *Physiology of Annelids*. Academic Press, New York
- Nunney, L. 1989.** The maintenance of sex by group selection. *Evolution* **43**: 245–257.
- Pascas-Gluzman, C. 1981.** A preliminary list of aquatic oligochaeta from Israel naididae and tubificidae. *Isr. J. Zool.* **30**: 230–232.
- Pianka, E. R. 1976.** Natural selection of optimal reproductive tactics. *Am. Zool.* **16**: 775–784.
- Precht, H., J. Christophersen, H. Hensel, and W. Larcher. 1973.** *Temperature and Life*. Springer, New York. 779 pp.
- Reznick, D. 1985.** Cost of reproduction: an evaluation of the empirical evidence. *Oikos* **44**: 257–267.
- Rowan, W. 1926.** On photoperiodism, reproductive periodicity and the annual migration of birds and certain fishes. *Proc. Boston Soc. Nat. Hist.* **38**: 141–189.
- Sauer, K. P. 1977.** Die adaptive Bedeutung der genetischen Variabilitaet der photoperiodischen Reaktion von *Panorpa vulgaris* (Mecoptera, Panorpidae). *Zool. Jahrb. Syst.* **104**: 489–538.
- Sauer, K. P. 1984.** The evolution of reproductive strategies as an adaptation to fluctuating environments. *Adv. Inv. Reprod.* **3**: 317–326.
- Sauer, K. P., H. Speith, and C. Gruener. 1986.** Adaptive significance of genetic variability of photoperiodism in Mecoptera and Lepidoptera. Pp. 153–172 in *The Evolution of Insect Life Cycles*. F. Taylor and R. Karban, eds. Springer, New York.
- Schierwater, B. 1989.** Allometric changes during growth and reproduction in *Eleutheria dichotoma* (Athecata, Hydrozoa) and the problem of estimating body size in a microscopic animal. *J. Morphol.* **200**: 255–267.
- Segal, E. 1970.** Light. Animals. Invertebrates. Pp. 159–211 *Marine Ecology*, Vol I, part I. O. Kinne, ed. Wiley, New York.
- Stearns, S. C. 1976.** Life-history tactics: a review of ideas. *Q. Rev. Biol.* **51**: 3–47.
- Stearns, S. C. 1980.** A new view of life-history evolution. *Oikos* **35**: 266–281.
- Stephenson, J. 1930.** *The Oligochaeta*. Oxford University Press, Oxford.
- Streit, B. 1978.** A note on the nutrition of *Stylaria lacustris* (Naididae, Oligochaeta). *Hydrobiol.* **61**: 273–276.
- Tauber, M. J., C. A. Tauber, and S. Masaki. 1986.** *Seasonal Adaptation in Insects*. Oxford University Press, Oxford. 411 pp.
- Townsend, C. R., and P. Calow, eds. 1981.** *Physiological Ecology. An Evolutionary Approach to Resource Use*. Blackwell Scientific, Oxford. 393 pp.
- Vershinin, N. V., and V. P. Semernoi. 1977.** Qualitative and quantitative characteristics of oligochaetes of the Krasnoyarsk reservoir. *Ekologiya* **1**: 105–107.
- Wetzel, M. J. 1982.** Aquatic oligochaeta in Kansas, USA, with notes on their distribution and ecology. *Tech. Publ. State. Biol. Surv. Kans.* **12**: 112–130.
- Zaslowski, V. A. 1988.** *Insect Development. Photoperiodic and Temperature Control*. Springer, Berlin. 187 pp.